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MICROBIOLOGY OF SEDIMENTS AND ITS GEOLOGICAL ASPECTS

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16. Abstract Sediment microbiology is a concern of both the biologist and the geologist. Bacteria influence the following more or less strongly and at a more or less advanced degree of diagenesis: 1. The organic matter in sediments and the final form in which it is found. 2. The anions CO_3^{2-}, HCO_3^-, NO_3^-, OH^-, SO_4^{2-}, PO_4^{3-} as well as their intermediate stages and the resulting minerals. 3. The cations H^+, NH_4^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, Fe^{3+} and a number of minerals which are dissolved or precipitated by microbial activity, as for example Fe, Mn, Cu, Ag, V, Co, Mo, Ni, U, Se, Zn. 4. Perhaps the silicon equilibrium. At least diatoms and radiolarians precipitate silica, while other reactions which have been proved are not yet shown to influence marine sediments. 5. Redox potentials and pH values of the sediment. 6. The composition of interstitial waters. 7. The surface activity of minerals, since bacteria grow preferentially on particle surfaces. 8. The energy flux and temperature of sediments. 9. The texture of fine-grained sediments. 10. The fossilization of microfauna, macrofauna and trace fossils. Sedimentology and mineralogy may also influence bacterial activity and the composition of the microflora within sediments. The Helgoland laboratory illustrates several difficulties met in research.

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MICROBIOLOGY OF SEDIMENTS AND ITS GEOLOGICAL ASPECTS

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Abstract /439*

The influence of bacteria on recent sediments was first discussed in 1885, when Fischer and Gazert were discussing the cycle of substances in the sea as well as in sediments. The influence of bacteria on the C, N, S, P and Fe cycles in recent sediments and the open sea was soon accepted by marine geologists. Nevertheless, only very few experiments have, so far, shown more than qualitative and quantitative data collection in various restricted areas. This is due to the extensive and complicated chain of reactions on the surface of sediments and in the sediment itself.

Biologists seek to determine the amount of organic and inorganic matter which is reworked and released to the sea. Geologists usually emphasize the amount of substances which are sedimented. For biologists the sediment is only part of their dominant ecosystem (the sea), while for geologists the "sea" merely furnishes and influences their true object of study, the sediment and the rock which is forming.

How much then, are bacteria involved in the slow process of conversion from a recent sediment to sedimentary rocks? Bacteria influence the following more or less strongly and at a more or less advanced degree of diagenesis:

1. The organic matter in sediments and the final form in which it is found.

*Numbers in the margin indicate pagination in the foreign text.

2. The anions CO_3^{2-}, HCO_3^-, NO_3^-, OH^-, SO_4^{2-}, PO_4^{3-} as well as their intermediate stages and the resulting minerals.

3. The cations H^+, NH_4^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, Fe^{3+} and a /440
number of metals which are dissolved or precipitated by microbial activity, as for example Fe, Mn, Cu, Ag, V, Co, Mo, Ni, U, Se, Zn.

4. Perhaps the silicon equilibrium. At least diatoms and radiolarians precipitate silica, while other reactions which have been proved are not yet shown to influence marine sediments.

5. Redox potentials and pH values of the sediment.

6. The composition of interstitial waters.

7. The surface activity of minerals, since bacteria grow preferentially on particle surfaces.

8. The energy flux into and temperature of sediments.

9. The texture of fine-grained sediments.

10. The fossilization of microfauna, macrofauna and trace fossils.

Sedimentology and mineralogy may also influence bacterial activity and the composition of the microflora within sediments. Methods and problems of sediment microbiology are demonstrated by some investigations in the German Bay (North Sea) in connection with the first German Underwater Station (UWL).

Ecological work proves to be difficult in various directions. The main causes of difficulties in microbiological work on sediments are the great variety of different factors influencing the environment (microbial, chemical, physical, mineralogical), the difficulty of taking representative samples, and the small amount of data which have been collected so far.

I. Introduction /442

The question of what bacteria actually do is just as old as microbiology. The question of what bacteria do in geological or geochemical terms is practically as old as modern bacteriology and intimately links our field of work with ecological questions. How do bacteria influence their environment, and what reverse effects does the environment have on bacterial colonization and activity? The portion of the environment which the geologist will look upon as his field of interest largely remains to his own discretion. He must realize, however, that microorganisms at least inhabit the object of the sedimentologist's study and actively affect it at many points. Bacteria range from the stratosphere to the greatest depths of the oceans. Bacteria have been detected in the lithosphere to a depth of 2000 m with some certainty. If we consider the "fixed" effect of "contemporary" bacteria on a sediment, the effects of microorganisms on the object of geological concern must also be extended to sedimentary rocks, which, though they are now buried deeper than 2000 m in the lithosphere, once harbored an active microflora. The cycle of substances (inorganic and organic) called "exogenous dynamics" thus extends beyond the recent life zone of the microorganisms.

The question of the effect of bacteria upon the cycle experienced by geologic materials was probably first posed by Schloesing and Münz (1877). Gazert (1886) and Fischer (1887) were first to work on marine-microbiology problems. They concerned themselves with the life of bacteria in and on recent sediments, with the accent on theoretical discussion of the issues vis-a-vis exact scientific data.

The earliest studies were followed by a number of studies which were concerned more or less intensively with the effect of bacteria upon sediment and thus upon oceanic geology. Some of these studies were soon discussed by geologists or carried out in close collaboration with geological researchers and published in geological journals. These include articles by Bavendamm (1932), Waksman (1937), Isacenko (1938), Zobell (1936), Baier (1935-1938), Rittenberg (1940), Halvorson and Starkey (1927, 1931), Hecht (1933), Harder (1919). In these first articles, data were collected, measurements which had been made were compared with bacteriological data, and the effect of bacteria on changes in the sediment were realized to be important. During the following years, oceanography developed in more and more specialized and numerous directions, the total view frequently being represented in the form of cyclic diagrams produced by the biologists, chemists and geologists. Even today, we have not progressed in all problem areas. The working methods have /443 sometimes been improved, and the data determined have become more numerous and in many cases more exact and more reliable. Many of the hypotheses proposed during the first flush of ecological research have been confirmed and augmented. A number of ideas had to be corrected, and other processes -- once they were recognized and demonstrated to be possible -- have still remained completely unexplained. Overall, it must be stated, on the basis of the present level of knowledge, that a large part of the processes taking place in recent marine sediments are still largely unexplained to the extent that they affect biological problems and chemical and physical problems which can be explained on the basis of biological processes. The three primary reasons for this lack of knowledge are the large number of variables involved (chemical, sedimentological and biological), the difficulty of obtaining representative specimens and relating them to the overall milieu, and the extremely sparse data -- in spite of the great many publications -- particularly concerning the microbiological content of sediments.

An attempt will be made in the following to provide an overview of the effects which the colonization of a sediment by microorganisms can have on the diagenesis and geochemistry of a sediment and on geology, and an indication of the data which have been gathered with regard to these problems. In addition, we will take a brief look into the methods of sediment microbiology and their reliability, and a special problem will be used to illustrate problem formulation in sediment microbiology or geomicrobiology.

II. Methods Used in Sediment Microbiology

The working methods of microbiology must vary as a function of problem formulation and object. The more specialized the object is -- the more it extends into physiological or genetic and molecular-biology areas -- the more precise the methods must be. The ecological/statistical approach was developed as it was discovered that bacteria participate in various basic conversion processes in nature. The initial point of departure was the fact that a specific microflora develops in each milieu and changes as a function of seasonal or other variations in the milieu. Thus attempts were made to obtain quantitative data on the distribution of microorganisms in the area under study. It was possible here to deduce directly the presence of bacteria on the basis of certain chemical processes which would not be otherwise explainable (theories on decay, nitrogen fixation, etc.).

Various methods were then developed and tested for determining the number of bacteria in a specific area: a) direct counting under a microscope; b) counting on plate cultures in Petri dishes with various solid nutrient media, on which a colony was assumed to arise from each viable microorganism; c) culturing in liquid media, in which the presence of bacteria is manifested by chemical changes in the milieu. Each of these possibilities /444
has its obstacles and problems. In long series of experiments

with a wide variety of media, in which the various methods were compared, it was found that the total germ count in a given area can never be determined exactly. All germ counts per unit of measure are dimensions of a statistical nature which represent reference values, rather than absolute information. For this reason, it is necessary that the methods used be standardized so that it will be possible to make comparisons and draw conclusions. The determination of germ count on nutrient medium 2216 E as described by Zobell has been adopted in marine microbiology as the most significant standardized method. This is a medium rich in organic, easily decomposed compounds (peptone, yeast extract) which is used in solid form to determine the number of heterotrophic bacteria. In easily converted liquid or solid form, it can be used to establish the number of microorganisms growing under anerobic conditions. Since colonies can only be counted at a certain density, the natural specimens are almost always diluted and each of the dilution stages applied separately to the medium and cultured. With the aid of statistical tables (from McRady) or parallel inoculations, it is then possible to obtain reliable numerical values which can serve as a measure of the colonization of a milieu by bacteria. This Zobell germ count method has been adopted worldwide and serves as the basis for ecological studies. In addition, various nutrient media can be utilized for the quantitative and qualitative determination of specific microorganisms. The ecologically oriented microbiologist is tending not so much to determine the quantity of a given species but rather to determine the quantity of microorganisms which are capable of a specific level of metabolic performance. Examples which we might mention are the conversion of organic material into inorganic compounds, such as the "ammoniation" of an amino acid, the oxidation or reduction of sulfur, the mineralization of phosphorus. Depending upon the method used, particularly in the determination of quantitative data, various difficulties arise in this approach which are already encountered in the study of waters but which are further intensified in the study of sediments. One problem is the avoidance of contaminants in the taking of specimens.

Quite well developed instruments already exist in hydromicrobiology. In the microbiology of sediments, we encounter the problem that it is precisely the microbiologically most active zone -- the sediment/water boundary -- which is very difficult to sample quantitatively. Germ count determinations performed on sediments have until now been made primarily with cores from plunger soundings (Rittenberg, 1940), Van'Veen samplers (Weyland, 1967) and grab-bucket specimens. Each of these instruments harbors problems for the microbiologist which stand in the way of a representative determination of germ count. In the case of sediment specimens which come from a relatively large core depth, the danger exists that contaminants will falsify the picture. In specimens which come from the sediment/ /445
/water interface, flushing occurs from above, into the first centimeters of the core. In addition, the surface can be partially destroyed while the instrument (grab-bucket) is being hoisted.

Reineck's large grab bucket has the advantage, however, that it brings up a large, relatively undisturbed surface, from which sufficient material for germ count determination, chemistry and grain size determination can be taken from the uppermost 4 mm. If, in addition to Zobell's germ count determination, we also wish to determine other physiological groups, we require a rapidly growing number of media, Petri dishes, test tubes, etc. We see from this that preparations for studying only one core sample take up 2 to 4 hours. This results in two decisive problems. The gross spatial capacity of a modern research ship is limited; the capability of monitoring several series, which normally must grow for 3 weeks and be counted, is reduced. To

this is added the statistically supported fact that the original germ counts change very rapidly (Zobell, 1946) when the specimen has been taken out of the ecosystem. The germ counts of water specimens begin to change after just 1 hour. Sediment specimens likewise change in microorganism content after just a few hours, although they maintain constant conditions somewhat longer, according to the few reference data obtained to date. Figure 1 shows various determinations of the number of microorganisms which decompose an amino acid with the formation of ammonia. /446
It follows from this that after just brief storage at room temperature and even when storage takes place at 4°C, the germ counts change very markedly. Experiments on specimens which were deep-frozen within 5 minutes, on the other hand, yielded rapidly decreasing germ counts, which decrease further with increasing storage time in the deep-frozen state. A requirement must therefore be that the microbiological analysis of sediment specimens be started within just a short time after sampling. The collecting of specimens, storage and subsequent analysis at the institute will thus be possible only in an extremely small number of cases. Physiological processes which affect the levels of inorganic substances continue even in deep-frozen cores.

Sediment specimens must also be homogenized prior to application to certain media (Gunkel, 1964). This is generally done with a mixing device which runs at high rpm, breaking up relatively large particles and washing the microorganisms off of surfaces with the resultant turbulence. A given weight of sediment is generally mixed with sea water in a ratio of 1:10 and treated for 1 minute with the Ultraturrax at 20,000 rpm. The result is an almost quantitative breakdown of aggregates and separation of the microorganisms from surfaces with the least possible killing of microorganisms. This suspension is then used to determine germ count in the form of a 10^{-1} dilution. Dilutions of up to 10^{-8}

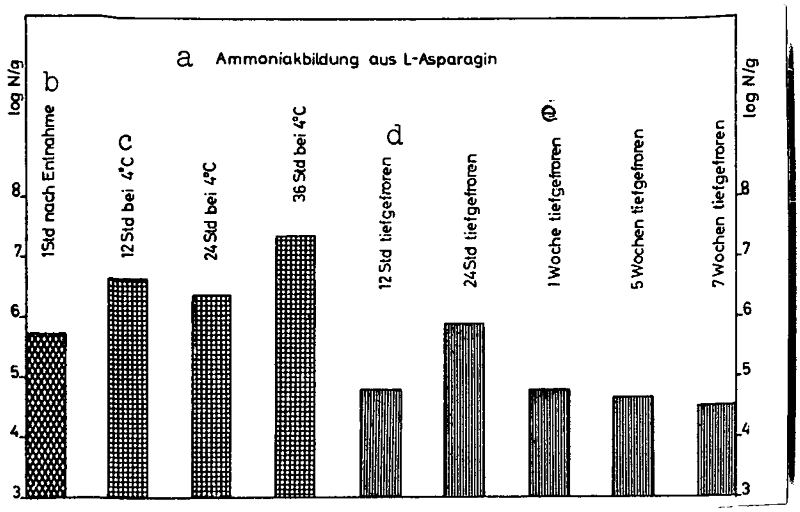

Fig. 1. Number of organisms forming ammonia from amino acids (heterotrophic bacteria), in log N/g (referred to dry sediment), after different storage times prior to workup. These processes can occur in all cores which have been stored for a relatively long time at 4°C.

Key: a. Formation of ammonia from L-asparagine
b. 1 hour after sampling
c. 12, 24, 36 hours at 4°C
d. 12, 24 hours deep-frozen
e. 1, 5, 7 weeks deep-frozen

must be prepared for active sediments with a high level of organic material in order to arrive at numerical ranges capable of evaluation.

A further obstacle in this method is the possibility that as the result of a slight change in the culture milieu or a single instance of contamination in the work, either no microorganisms are detected where some are certainly present, or too many microorganisms are determined because they have been carried along in the dilution process.

The interested geologist can obtain a more exact overview of the oceanomicrobiological method in the section on bacteria by Gunkel and Rheinheimer in Schlieper (1968) or in Zobell (1946). Problems in the systematics and the selection of culture media are also treated by Brisou (1955). Additional textbooks and articles on marine and sediment microbiology are referred to in Wood (1965) and Schlieper (1968). The literature prior to 1946 is cited en bloc by Zobell (1946).

For the geologist who concerns himself in greater detail with microbiological effects on his object of study, sediment, he will find the following points important: 1. The specimen must be worked up microbiologically immediately after sampling. 2. Even though it is desirable to work up the largest possible number of specimens in dealing with ecological problems, the possibilities are limited.

III. Effect of Microorganisms on Geological Objects, and Geological Problems in Sediment Microbiology /447

Today, it is self-evident that sedimentological and general geological problems exist which can be solved with the aid of microbiology. There is general agreement, moreover, that certain parameters in sedimentology result from, or are markedly modified by, the activity of microorganisms. The following quote from Geologische Rundschau 29 should illustrate how difficult collaboration between the two fields is to implement and how little progress has been achieved in the results obtained in sediment microbiology:

"It may at first seem strange if we insist that problems exist which are of considerable general interest to geology and bacteriology. If we think not so much about the fossilization of bacterial cells themselves as about the geochemical significance of their metabolism, however, we will be less inclined to suggest that such a statement is exaggerated. It has been necessary that both sciences achieve a certain level of development before they came into contact. Geology saw itself faced with the necessity of effecting an understanding of subaquatic fossil sediments through research on recent underwater soils and their origin and alteration. Bacteriology had to extend its range of research beyond its original medical/technological onesidedness and include bacteriological research on bodies of water and the ocean floor.

The beginning of hydrobacteriological research and of research on current hydrogeological phenomena marked the first points of contact between the two sciences."

This quote is now 33 years old (Baier, 1937). Our knowledge has since increased, our methods have been refined and developed; still, we are just as far as ever from achieving an overall view with quantitative information. Baier developed his ideas in 1937, and sediment research and the geology of current processes actually made great advances. Unfortunately, we can still practically count the number of sediment-microbiology articles in the area of the North and Baltic Seas on one hand. Joint projects between geologists and microbiologists are even rarer. An example of one start is the joint publication (Koske, Rheinheimer, Krumm, Szekielda, 1966) on the sedimentation and bacteria content of the Elbe.

Outside Germany, the number of bacteriological projects which covered sedimentological and geological problems or have been able to elucidate geological problems has increased markedly. The geologist's field of view has brought forth geochemical results on bacteriological processes. In a number of cases, it has been possible to provide definitive evidence of a quantitative nature for the influence of microflora on recent sediments and thus, by inference, on sedimentary rocks and sedimentary deposits. Nevertheless, there is vigorous disagreement, and articles are still appearing, and will continue to appear, which, with a geological or bacteriological point of view, totally overlook the close link between the two areas. Between them lies the broad field of effects on sediment caused by physicochemical processes and by /448 microfauna and macroflora. Between them also lie the geobiochemical and organic-chemistry studies on recent sediments, which are becoming more and more important and provide a bridge between microbiology and geology. Anyone wishing to go into this problem area in greater detail will have to refer to summaries such as those provided by Zobell (1946), Abelson (1963), Degens (1968), Emery (1960), Kuznetsov (1963), Silverman and Ehrlich (1964), Rogoff (1962), Davis (1967) and Zajic (1969).

The part of the exogenous cycle which is concerned with completely formed sedimentary rocks and their further development will only be mentioned here as the processes of a microbiological nature which are involved in transformation are frequently operant both in the area of oceanic geology and in the areas of soil science and exogenous dynamics (Silvermann and Ehrlich, 1964; Kusnetsov, 1963; Krumbein, 1969). An attempt will be made in the following to summarize the points of contact between sediment microbiology and geology and illustrate the present level of development as well as possible. The ultimate goal of all microbiological studies which can provide the geologist with important information should be the calculation of quantitative indices such as nitrate turnover / cell per unit time for a known cell count / / sediment volume.

a) Origin of Life in the Ocean and "Evidence" of It in Sediment

We will consider this topic, which has found more and more attention in the widest circles, due to its popularity, in very brief form, merely for the sake of completeness. If we disregard doctrinaire philosophers of science whose publications are usually based not so much on scientific information as upon an arbitrary representation of the gaps in our knowledge and natural-philosophy and metaphysical writings, then the presently available material and the conclusions which we can draw from laboratory experiments indicate a time interval in the Precambrian from which we have found sediments that contain 1. organic material and 2. structures

which, with great caution, can be interpreted as single-celled microorganisms, of which some are occasionally arranged in chains, small clusters, or patterns otherwise typical of microorganisms. The sources of error and possibilities for misinterpretation are great. However, conscientious studies such as those by Barghoorn et al. (1965) or Prashnowski et al. (1967) and surveys such as by Bernal (1961), Welte (1967) and Oberlies and Prashnowski (1968) indicate that organic substances and organized microorganisms can be considered the first fossils. The theories of stages and the experimental foundations for them are provided in very summary form by Bernal (1961). He assumes that ammonia, carbon dioxide radicals and HS compounds were initially formed. The first compounds which reproduced in a more or less random manner are then assumed to be coacervates and polymers of amino acids, pyrimidines /449
and peptides, which can be produced inorganically, as various researchers have demonstrated. The first reactions which can be interpreted as metabolic processes would then be dehydrogenation and anerobic fermentation. At this point so-called eobionates appear, i.e. protein-coated organelles and coacervates which can not be considered living forms. From these developed the protobacteria, at first randomly via catalytic and uncontrolled reactions (particularly in contact with sediment); these are essentially distinguished from their precursors by precise copying of "functioning" nucleic acids once they have formed. From this moment on, life processes -- for a long time, only microbiological processes -- affected inorganic development and the character of sediments. We should consider the fact that wherever a macrofauna and macroflora are absent, for whatever reason, the microflora develops as the dominant form and can determine the character of the milieu (Krumbein, 1969).

The first stages in the development of life are thus intimately connected with the question of the hypothetical metabolism of hypothetical microorganisms. Two principal directions must have developed early here: 1. Introduction of photosynthesis and metabionts which take their energy for reproduction from photosynthesis and 2. chemosynthetic metabionts, which take their energy from controlled chemical oxidation-reduction steps and reproduce along this pathway. The first path is bound to the atmosphere/water interface; the second, largely to the sediment/water interface. It appears reasonable that photosynthetic processes also started at the sediment/water interface at places where sunlight reached it.

b) Effect of Microorganisms on the Organic Content of Sediments and the Ultimate Form in Which It Occurs

As stated under a), simply and also more highly organized organic compounds can be synthesized in abiological processes. There is now no doubt, however, that approximately 100% of the organic materials in sediments and sedimentary rocks are of biological origin. Its further development can be determined biologically and physicochemically. The organic content of sediments stems from the biological activity of the column of water over the sediment and biological activity within the sediment itself. Although macroorganisms have in many cases been found living in certain sediments at depths of up to 2 and 3 m, it can be stated that the activity of macroorganisms is restricted almost completely to the first centimeter of sediment. The same applies basically to microorganisms. There are cases, however, in which microorganisms participate actively in the further development of organic material in the sediment where these sediments have already been shifted to considerable depths.

The effect of microorganisms on the organic content of sedi- /450
ments culminates, as far as the geologist is concerned, in the following principal topics:

1. Genesis and subsequent development of petroleum;

2. Effect upon the return of organic substances into the open water from sediment;

3. Effect of microorganisms on the inorganic composition of sediment, via changes in organic and inorganic makeup.

The subsequent history of petroleum and of the organic content of sediments can in many cases also be affected by abiological processes. Thus the question of a quantitative demarcation between biological effects and abiological effects is an important one.

These questions have been the subject of extensive work by Trask's study group (1926-1941) from the American Petroleum Institute. Projects 43 A (directed by Zobell) and 43 B (directed by Whitmore) were primarily concerned with the effect of microorganisms on the development of the organic content of sediments. These projects have also been continued in recent times by a large number of other researchers. It has now been ascertained, as a result of this research, that petroleum and substances similar to petroleum occur to a much wider extent, in extremely small concentrations, throughout sediments than are ultimately accumulated in deposits which are really workable. Since microorganisms are in almost all cases the last "processors" of organic substances in the biological cycle, bacteria, algae, fungi and actinomycetes come under primary consideration for biological effects on the organic material from which petroleum is ultimately formed. It is now largely agreed that petroleum develops in sediments and that microorganisms are involved qualitatively and quantitatively in all stages of petroleum generation (Davis, 1967; Abelson, P.H., 1963; Azoulay, E., et al., 1962; Beerstecher, 1954; Clark, R.C., et al., 1967; Degens, E.T., 1968; Evans, W.C., 1963; Oppenheimer, C.H., et al., 1965; Orr, W.L. and

Emery, K.O., 1956; Seyer, W.F., 1933; Smith, P.V., 1954; Stone, R.W. and Zobell, C.E. 1952; Trask, P.D., 1939; Zobell, C.E. 1943). It is impossible to go into the individual steps in the synthesis and degradation of hydrocarbons and carbohydrates here which have been detected in recent sediments in microbiological research. It is sufficient to say that the organic material originally present can be transformed by microorganisms in the direction of the composition of petroleum deposits but, on the other hand, that starting from the same composition of orgânic material in recent sediments, a large number of purely physicochemical steps also make the same development possible.

The question of the origin of petroleum-like substances in sediments is only one aspect of the relationships between organic materials and sediment. The organic material in sediments and the microbiological processes which occur as a result can also have an effect upon other processes in the development of sediments. A close relationship exists between microorganisms, /451
organic material and clay minerals. Stotzky (1967) and his coworkers have ascertained that clay minerals have a remarkable, selective capability of adsorbing bacteria and fungi. I.e., the presence of clay minerals in a sediment results in the enrichment of microorganisms, particularly on the surfaces of clay minerals. Novakova (1968) has in turn concerned herself with the microbiological utilization of hydrocarbons and substances containing N. She arrived at the result that certain clay minerals accelerate the mineralization of hydrocarbons by bacteria. On the other hand, there are projects which indicate that organic substances are adsorbed so strongly to clay minerals (sometimes in intermediate lattice layers in mixed-layer clay minerals) that they may no longer be accessible for further degradation by microorganisms. It is possible, moreover, that the bacterial colonization of clay minerals and the associated presence of

organic substances can also affect the texture of sediments which are rich in clay minerals. Mattiat's work (1969) may elucidate such questions.

Microorganisms also have a decisive effect on the liberation of soluble organic compounds from the biodetritus and on the mineralization of organic compounds and their release into pore water and the column of water above. Detailed studies are available on this problem area (Zobell, 1946; Carey and Waksman, 1934; Evans, 1963; Gunkel, 1962; Hecht, 1933; Kutsnetsov, 1968; Rittenberg et al., 1955; Waksman and Hotchkiss, 1937, Zobell, 1942; and many others).

Also of considerable interest here is the extent to which phosphates which are organically fixed are liberated again into the water, and whether the mineralization of phosphate forms one of the principal sources for the supply of nutrients from relatively great water depth. This appears to be true in many cases (Hayes, 1963, in Marine Microbiology, Oppenheimer, ed.). On dry land, too, a large portion of the phosphorous fixed in organic material is liberated again by bacteria (Tardieux-Roche, 1966). Articles on the nitrogen cycle, the carbon cycle and the sulfur cycle exist in such large numbers that the geologist will only be referred here to the summarizing works (Zobell, 1946, Oppenheimer, ed., 1963; Kutsnetsov, 1968, etc.).

Regarding the content of mineralizable P, N, C and S compounds in the total organic material, it is an important fact that the amino components and a large portion of the sugars can be very rapidly degraded again and returned to the cycle of substances in the ocean. Higher hydrocarbons and cyclic compounds are indeed likewise degraded and broken open, but are more inclined to condense and to polymerize into larger complexes. The humus substances in the soils and their relationship to the activity of microorganisms have recently been described and classified in an outstandingly detailed manner (Kononova, 1961). The fraction of sediments and sedimentary rock of similar composition, so-called kerogen, has not yet been studied in such detail, and the conditions which result in its origin and formation are far from being known in detail. On the other hand, 90-97% of the organic material which is present in older sediments and in sedimentary rocks at all frequently occurs in the form of kerogen. The ratio between the individual elements in the humic acid or kerogen fraction is approximately 55:35:5:5 in the order C;O:H:N. This means that nitrogen has been lost relative to the fraction in the organic material initially supplied. Nitrogen is primarily fixed in the amino compounds, which can very easily be degraded again. Bacteria generally prefer acidic amino acids as a source of nitrogen, for which reason the basic components of the amino acid fraction are frequently retained longer. /452

It is impossible, in such a survey, to give a detailed treatment of the quantity of information which is already available on the relationships between organic material and microorganisms. A number of experiences will be pointed out which may be of importance to the sedimentologist.

1. The milieu in which the sediments have been deposited affects the microflora and likewise the type and composition of organic compounds incorporated in the sediment accordingly, and the latter in turn interact with the microflora.

2. The microorganisms in an ecosystem -- i.e. a given sediment -- are dependent upon and influence one another.

3. The type and composition of microflora fluctuate as a function of sediment type.

4. The chemical activity of heterotrophic bacteria is primarily a function of the type and quantity of organic material present.

5. The chemical activity of autotrophic microorganisms -- i.e. those which are independent of organic material -- is primarily a function of the composition of the sediment and of the pore water.

6. The interactions between individual organisms are sometimes so intimate that we could speak of them as symbiotic processes.

7. Colonization of the upper centimeters of a sediment and the chemical reactions associated with this are very much a function of oxygen concentration, of redox potential and thus of related metabolic processes. The mineralization of organic compounds results in oxygen depletion in the sediment. The oxygen content of 400 m^3 sea water is required for the biological degradiation of 1 kg petroleum. Particularly the fine-grained sediments deposited under calm sedimentation conditions are depleted very rapidly in oxygen and have highly negative Rh values. The redox potential of a specific sediment is not only a function of grain-size distribution, water covering and water motion but, /453
to a large degree, also of the activity of the benthic fauna and flora, particularly the microflora (Zobell, 1946; Hickel and Gunkel, 1968; Krumbein, 1970 (in press); Rittenberg and Orr, 1955; Oppenheimer, ed., 1963 and 1968). These processes result in a decisive superimposition of geological effects on the sediments, which is also manifested by the rocks which develop from them.

The colonization of sediment by microorganisms with increasing depth is also related to these questions. Colonization generally decreases with increasing depth (Zobell, 1936; Rittenberg, 1940; Rittenberg et al., 1963; Kutsnetsov, 1963; Krumbein, 1970). To be sure, a high percentage of heterotrophic microorganisms which live in the upper millimeters of the sediment are capable of maintaining their metabolism even without oxygen. They are facultatively aerobic as opposed to obligatorily anaerobic bacteria.

A still unsolved problem is presented by the studies of relatively long sediment cores in which strata almost completely free of microorganisms alternate with strata of high activity, even at relatively great depths. These data indicate, however, that the activity of the microflora is not generally restricted to the uppermost parts of a sediment.

c) Effect of Microflora on the Mineral Content of a Sediment

1. Carbonates: The problem of the carbonate cycle and carbonate equilibrium in the marine milieu has been treated by such a large number of authors that it is almost superfluous to contribute here. We find it disquieting, however, that the effect of the microflora on the carbonate equilibrium is referred to either not at all or in a merely catchall manner, and sometimes referred to as insignificant, in many summarizing reports on the geochemistry of carbon (Degens, 1968; Krauskopf, 1967; Wedepohl, ed., 1969). This means that three areas of work more or less side by side arrive at results which do not contradict one another but which achieve only conditional inclusion in the summarizing literature. The classification of carbonates as biogenic and nonbiogenic carbon compounds by Craig (1953) and other authors yields information only about the carbonates which have passed through the metabolism of an organism. No doubt exists today that a large number of macroorganisms and algae fix

and precipitate carbonates biochemically and that this carbonate pathway can be demonstrated via isotope distribution (Vogel, 1960).

Many microbiologists and geochemists have pointed out time and again, however, that microorganisms can precipitate quite considerable quantities of carbonate that is not fractionated in the cell but is precipitated outside the cell by the metabolic activity of the microorganisms and the resultant changes in pH, redox potential and the concentration of sulfate, ammonia, iron, phosphate and hydrogen. The same applies to the dissolution of carbonates (Baier, 1937; Bavendamm, 1932; Berner, R.A.; Cloud et /454 al., 1962; Greenfield, 1963; Jarke, 1949; Krumbein, 1968; Lalou, C., 1957; Oppenheimer, 1961, 1960; Russel et al., 1967; Silverman and Ehrlich, 1964). Closed carbonate systems are frequently treated in the geochemical literature on the carbonate problem. It must be repeated that recent sediments do not form a closed system and that carbonate dissolution and precipitation run counter to the physicochemical rules at so many points that an effect by microbiological reactions on this equilibrium could have been derived on the basis of this, alone, if the above-mentioned authors had not provided evidence in laboratory experimentation.

2. Sulfur: Many excellent articles on sulfur and its cycle in nature have appeared in the geological, geochemical and microbiological literatures. It is clear that sulfur compounds play an important role in sedimentology, due to the high sulfate content of sea water. If information concerning every element were so complete and precise as that on sulfur, many problems of marine geology would be considerably closer to solution. The isotopic chemistry of sulfur has been studied in an outstanding manner, many steps in the biological sulfur cycle are known very exactly, and the geological effects of the sulfur cycle in nature have been covered many times in summarizing reports.

Since general knowledge of the sulfur cycle in nature can be assumed, we will go into various open problems here. We can assume that of the six oxidation states of sulfur, the sulfate ion is the most stable in the presence of oxygen. In the absence of oxygen and the presence of heavy metals, the heavy metal sulfides of oxidation states -1 and -2 are the stablest and the most frequently distributed. All states lying between these, and their compounds, can occur briefly in nature and can be demonstrated in the microbiological sulfur cycle as intermediate stages or end products of metabolism. The deposits of elementary sulfur are largely of volcanic origin, but frequently have microbiological processes superimposed on them. Cases of sulfur deposits of microbiological origin are also known (Kutsnetsov, 1963; Silvermann and Ehrlich, 1964).

It can be stated, most briefly, that microorganisms oxidize and reduce sulfur and that sulfide and sulfate are produced by microorganisms from organic sulfur compounds. These processes occur continuously in sediments and contribute more or less to the ultimate composition of a sedimentary rock (Zobell, 1963; in Breger (ed.); Baasbecking et al., 1961; Butlin, 1953; Kaplan and Rittenberg, 1964; Oppenheimer (ed.), 1963; Postgate, 1960; Suckow, 1956; Starkey, 1953, Trüper, 1969). The microbiological effect on the sulfur compounds in a sediment is limited in terms of isotope composition and the differences in δS^{34}. The disagreement between Kaplan and Craig concerning the interpretation of heavy /455 metal enrichment in the area of hot brines in the Red Sea shows, however, that questions regarding the sulfur cycle can remain unsolved in spite of the collaboration of microbiologists (Trüper), geochemists (Degens, Hartmann, Craig, Bischoff) and nuclear chemists (Kaplan, etc.). Hartmann and Nielsen (1969) also point out that various unsolved problems exist in the chemistry and microbiology of sulfur in sediments. The continual inflow of sulfate ions into interstitial water, uncertainty regarding the extent of H_2S liberation from organic compounds, and difficulties in the methods of microbiological analysis of sediments result in the fact that a number of detailed studies are still required before we can become thoroughly familiar with all sulfur pathways in the sediment and can express them in quantitative indices. The problem of the transformation of iron sulfides of various types into pyrite and the factors involved have been discussed in detail in the articles by Love (1957), Love and Amstutz (1966) and Berner (1964).

3. Heavy metal sulfides and oxyhydrates/oxides in sediments: Sediment microbiology is unfortunately one direction in research which achieves only a small number of data on the ecology and chemistry of recent sediments at relatively high cost. Interpretation of the as yet sparse data must therefore always be supported by parallel laboratory experiments.

Almost all heavy metal sulfides in recent sediments have been fixed via the reduction of sulfates or the liberation of H_2S from organic sulfur compounds. It may be that such extreme cases as the hot brines in the Red Sea provide an indication of workable sulfide deposits with no biological effects. On the other hand, an extensive literature indicates that fossil heavy metal sulfide deposits such as the Mansfield copper shale may also be intimately connected in their genesis with the microbiology of sediments. Since Schneiderhöhn's observations and the discovery of autotrophic sulfur organisms by Beijerinck, discussion in this regard has continued to reappear in the geological literature. We can now state with certainty that the biological genesis of this type of deposit has been demonstrated unequivocally (Suckow, 1965). Microbiological processes and biochemical and colloid-chemistry consequences of microbiological

effects on sediments also make it possible to conclude that the enrichment and precipitation of Ag, As, Bi, Ca, Cd, Co, Cu, Fe, Mg, Mn, Mo, Ni, Se, U, V and Zn are frequently related to the activity of microorganisms. The autolysis of living organisms without the direct participation of bacteria, fungi and actinomycetes cannot explain this fixation of metals in sediments and their enrichment far beyond thermodynamic equilibrium. In this regard, Liesegang's observations, to the extent that they relate to fractionated precipitation about organic cores, must be subjected to a microbiological check just as much as the articles by Hecht (1933), Seibold (1962) and Hartmann (1963), who, to be /456
sure, clearly refers in his discussion of instances of vanadium enrichment to the reducing action of organic material alone and of the microorganisms living from the organic material. The literature on the dissolution and precipitation of minerals by microbiological paths has been discussed in detail by Silverman and Ehrlich (1964). Additional microbiological work on the iron equilibrium has been provided by Baasbecking and Moore (1959), Baier (1935), Butkevich (1928), Halvorson and Starkey (1931), Harder (1919), Perlman (1965), Starkey (1945).

The precipitation of manganese in aqueous medium has been studied in detail by Bromfield (1950). Other authors have also concerned themselves with the question of manganese enrichment in sediments or on the surface of sediments. The question of microbiological precipitation is also touched upon in the discussion of the origin of manganese nodules on deep ocean floors. No extensive microbiological studies have yet been made in this regard, however (Baier, 1935; Butkevich, 1928; Kutsnetsov, 1963, p. 177; Buser and Grüttner, 1956; Schweisfurth and Gattow, 1966; Krumbein, 1969; Schweisfurth, 1969).

Various other metals of less significance or of generally lower concentration in the sediments can become highly enriched by the action of chelate-forming substances, by adsorption on microorganisms, and by microbially generated acids. Literature on this complex of problems can be found primarily in Silvermann and Ehrlich (1964) and Perlman (1965), Schalscha et al. (1967) and in Zajic (1969).

The precipitation of oxide hydrates and oxides from aqueous solutions by microorganisms has frequently been observed both in fresh water and soil and in sediments and can result in deposit formation in many cases. Thick iron hydroxide and manganese hydroxide precipitates occur in the autolysis of phytoplankton algae and also in the case of Myxophyceae. To this is added the effect of bacteria in the iron cycle, which has been represented schematically by Kutsnetsov (1968) and was treated in detail even earlier by various authors (Mulder and van Veen, 1963; Baier, 1935; Sokolova, 1961).

4. Silicon: Silicon plays such a dominant role in sediments that we must consider it at least briefly. An extensive geochemical literature exists on the silicon equilibrium in pore waters and sediments, which is of interest primarily because of the low solubility of Si. We know that at the time of plankton bloom, Si can become the growth-limiting factor for diatoms and that the supply from solid land and mixing in the underlying water can compensate for the silicon deficit at the surface. We likewise know that many silica deposits can be attributed to diatoms and Radiolaria. But there is as yet no explanation for a large number of high-silica sediments which occur in the history of the earth. Sediment microbiology can likewise provide no indication here to date. It is certain, however, that microorganisms can dissolve silicic acid from silicates, from amorphous silica gel and from quartz (Oberlies and Pohlmann, 1958; Krumbein, 1969). Heinen (1960) has shown that Si can be /457

fixed in bacterial cells in place of phosphate. He likewise points out that Si is probably also fixed on the mucopolysaccharides of the capsule. Oppenheimer and Master (1963) point out the relationships between Si and CO_2 in biogenic substances. Reifenberg and Buckwold (1954) show that Si can be taken from the soil via the orthophosphate ion; Correns (1950) has developed a scheme according to which the relationship between the solubilities of Si and carbonates could result in the formation of silica gels. Siever and Scott (1963) provide an indication that differences in alkalinity produced by bacteria or organic material can lead to the dissolution and precipitation of silica gel. Weeks (1953) proposes this mechanism for the origin of carbonate concretions in claystones. That silica gels could arise via a microbiological effect on the milieu of sedimentation can neither be ruled out nor unequivocally verified at the present state of knowledge. The widespread cherts of the Precambrian are often linked with organogenic sediments, however, and contain rich traces of microorganisms (Barghoorn, 1965; Oberlies and Prashnowski, 1968). Pronounced changes in the milieu of sedimentation and related rapid variations in the microbiological ecology could result in pH values and redox potentials which would explain the banded siliceous shales.

d) Effect of the Microflora on the State of Preservation of Fossils and Disturbed* Structures

It will only be briefly mentioned here that microorganisms can participate to a considerable degree in the destruction or preservation of fossils. Hecht (1933), Mesebach (1952), Voigt (1950) and Wetzel (1938) have concerned themselves with these problems in detail. Various other authors have likewise treated

*[Translator's note: The German root used here means "dig," "delve," "stir up," "root."]

the problem of burst carcasses, more or less completely mummified animal bodies, the presence of fossilized microorganisms in animal and plant tissue, and related questions. The most beautiful pictures of traces of feeding and effects of microorganisms on fossils have been obtained by the varnish-film method in work on the Miocene in the Geisel Valley.

In this regard, it is worth mentioning the extensive discussion concerning the pyrite spheres (framboidal pyrite) in recent and fossil sediments which were first interpreted by Schneiderhöhn and later by Love (1957) and others as mineralized bacteria. Vallentyne (1963) later demonstrated that these spheres, with diameters between 1 and 40 μm, can also be formed in the shells of small foraminifers and other animals. Love (1966) then corrected his original ideas. In principle, it is of no importance, however, whether mineralized bacteria or bacterially generated sulfides are involved. The development of pyrite from bacterially precipitated iron sulfide occurs at a very early date, according to the above-mentioned authors, and the resultant mineral aggregates can have precisely the same form as raspberry-shaped /458
aggregates which have been produced completely inorganically. The important realization is that pyrite is detectable very soon after the generation of H_2S and the precipitation of iron sulfides. Pyrite may even be produced simultaneously with iron precipitation by sulfurous bacteria.

e) Sediment-Microbiology Work in German Waters

Sediment microbiology is of course an integral component of hydromicrobiology. To be sure, the problems, the methods and the effects on other sciences are sometimes quite different. A number of projects have already been mentioned in the introduction which were applied to sediments of the Baltic Sea or North Sea. To these are added a number of publications which are aimed in physiological, systematic and biochemical directions and are only linked with the German oceanic areas via the isolate.

Pure sediment-microbiology projects have unfortunately been very limited in Germany until now.

The work done by Baier, who provides a survey up to 1938 in his article in the Geologische Rundschau, is of primary importance to the development of hydromicrobiology with regard to sediment research. Hydromicrobiology has been applied to a greater extent in Germany since 1950; we must sometimes separate the projects in lakes from the oceanographic work. Earlier projects on marine microbiology stem primarily from the Institute of Microbiology of the University of Kiel, the Microbiology Department of the Helgoland Biological Laboratory, and the Microbiology Department of the Institute for Oceanic Research of Bremerhaven. Work on the sediment microbiology and sediment chemistry of inland waters has been conducted at the Max Planck Institute of Hydrobiology in Plön and the Biological Institutes at Lake Constance.

A number of detailed projects on the sediment microbiology of the North and Baltic Seas have been carried out recently for the first time (Hickel, 1968, 1969; Weyland, 1967; Koske et al., 1966; Overbeck, 1968; Gunkel, 1962; Dietrich, Höhnk et al., 1960 and 1965; Krumbein, 1970 (in press)).

Articles on special problems in sediment microbiology stem from the Institute of Microbiology of Greifwald (W. Schwartz and coworkers). One of the most interesting for the geologist is the article by Suckow (1965) on the genesis of the Mansfield copper shale, as well as the articles by Wagner and Schwartz (1963).

The author is presently concerned with problems of methodology in sediment microbiology, with the detailed recording of bacterial levels in the sediments of the North Sea with respect to the interaction between microflora and sediment, and with the effect of the microflora on the grain fraction below 63 μm and the effect of this fraction on sediment colonization. During the course of this work, it proved to be more and more difficult to keep the overall milieu in view, due to the large number of detailed problems.

The difficulty of obtaining unequivocal results and a knowledge of the processes in recent sediment will be illustrated with the studies performed during the initial use of the underwater laboratory at Helgoland. /459

f) Studies on the Colonization of Sediments by Microorganisms in the Vicinity of the Helgoland Underwater Laboratory

Microbiological studies were performed in the first experimental work on sedimentological and oceanic-biology problems utilizing permanent underwater structures in Flensburg Cove in the autumn of 1968 and at Helgoland in the summer of 1969. These studies will be covered in greater detail elsewhere. The data obtained in these projects provided information of interest to the geologist regarding the colonization of sediments by microorganisms and regarding the problem of methodology in joint microbiological/sedimentological studies. The location of the Helgoland underwater laboratory (UWL) has been plotted in Fig. 2. A precise comparison between directly sampled sediment specimens and specimens taken from shipboard by grab bucket could be made for the first time in the UWL studies. Figures 4 and 5 show the result of this test. It was found here that a specimen taken by a diver at the floor of the ocean with the aid of a sterile Petri dish yielded results which were higher in all values than the grab-bucket specimens. This indicates that, in spite of great caution in sampling, the water/sediment interface is not brought up quantitatively by the grab bucket. It must at least be assumed that water and thus extremely small particles infiltrate the sediment on the way up, and thus bacterial distribution and the organic material at the interface are subjected to changes caused by the sampling process.

While the aquanaut team was in the UWL (time period of experiment: July 28 to August 19, 1969), specimens were taken from five locations at regular intervals by a diver. The author, as a surface diver, transported these specimens to the laboratory immediately after sampling whenever possible. Occasionally this was not possible, due to the differences in time breakdown. In such cases, the specimen containers were left in the sampling area. It was found here, however, that although the sealed Petri dishes were also tied in plastic bags, they were moved so vigorously in the current that instances of washout occurred similar to those in the case of grab buckets.

Figure 3 shows the distribution of individual locations over the area of operation. Since the aquanauts could not leave their area of operation (delimited by the laid-out lines), because the danger of straying could lead to fatal accidents, location 5 was approached by the diver from the surface, and the specimens were taken directly to the laboratory.

Location 1 was under the so-called igloo, an observation /461
station based on the principle of the diving bell. The igloo stood on two large concrete blocks, between which a current channel formed (during ebb and flow) that produced large ripples at the particular end of the tunnel within 12 hours. The specimens were taken from these ripples. This involved a quite

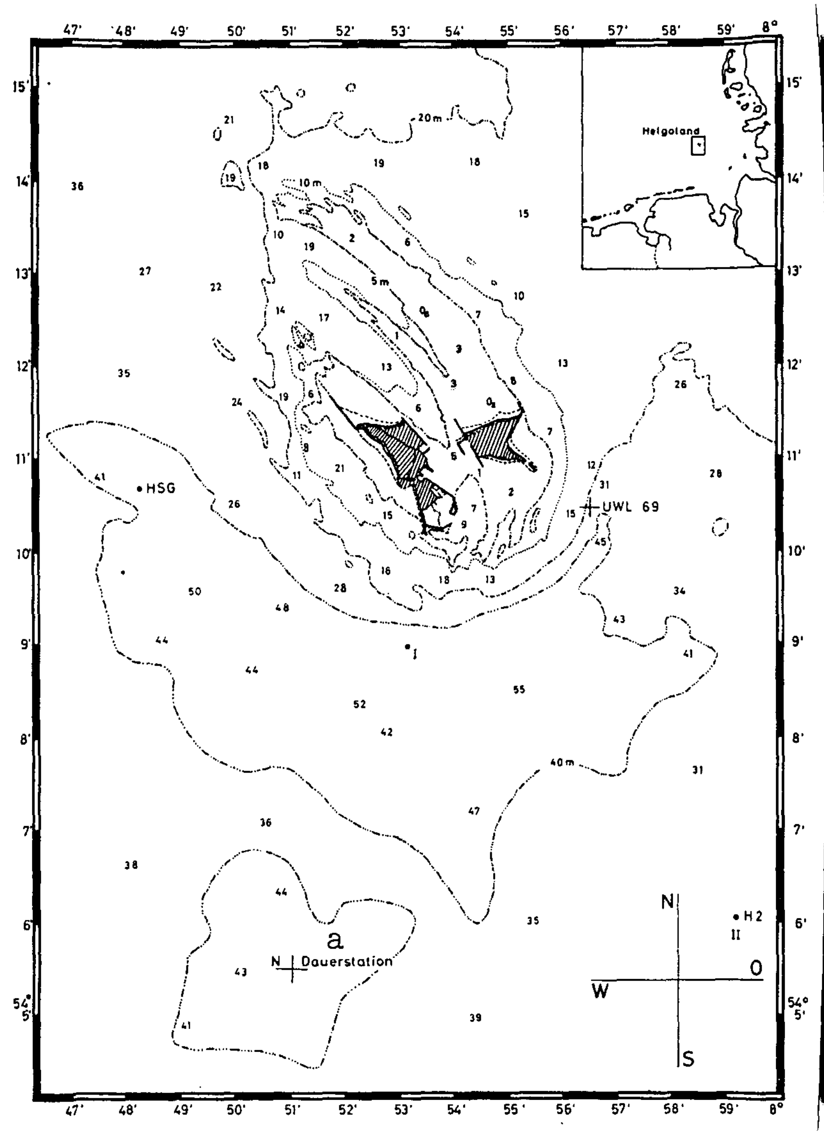

Fig. 2. Map of the ocean area around Helgoland with the location of the Underwater Laboratory, the permanent station at which the sediment microflora is being determined routinely every 3 weeks, and three stations (HSG, I, II) on the more frequently traveled profile of special interest, along which sediment-microbiology studies are being conducted.

Key: a. Permanent station

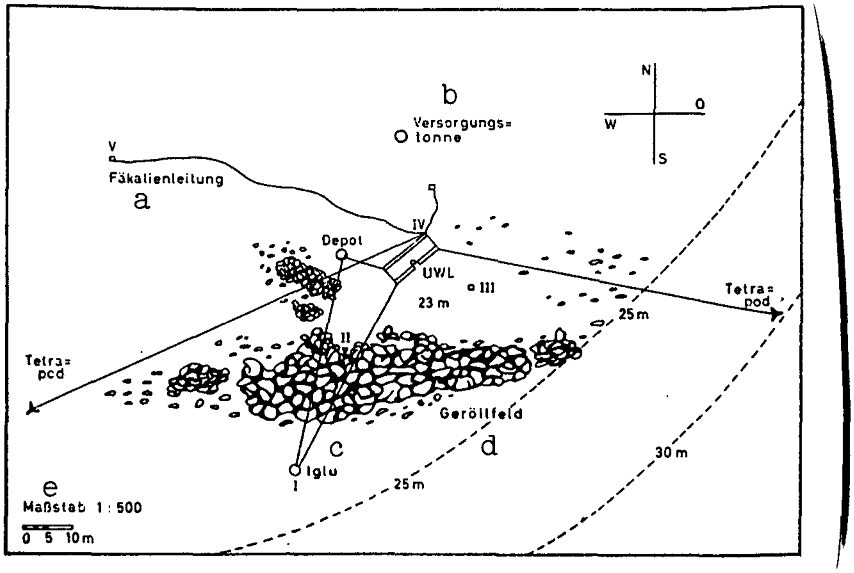

Fig. 3. Map of the immediate study area of the Underwater Laboratory, with the stations used for sediment-microbiology studies.

Key: a. Sewage line
b. Supply buoy
c. Igloo
d. Boulder field
e. Scale

freshly relocated sediment, in the case of which it was questionable whether bacterial colonization would not be disturbed. In spite of the intensified current through the obstacle, however, no basic change occurred in grain-size distribution, which was similar throughout the area, aside from differences in the amounts of perch* and oyster shells which were mixed in.

Location 2 was in a small "bay" at the edge of the boulder field. The sediment was very soft, loosely stratified, and it was possible to penetrate up to one's wrist or deeper without effort at many points, although the maximum in the grain-size curve was in the 0.25-0.16 mm range. During periods of slack

*[Translator's note: Apparently a typographical error in the original.]

water, there was a considerably more pronounced increase in freshly sedimented floccules could be observed relative to the other stations. These bays were also preferred stopping places for flatfish and Eupagurus bernardus.

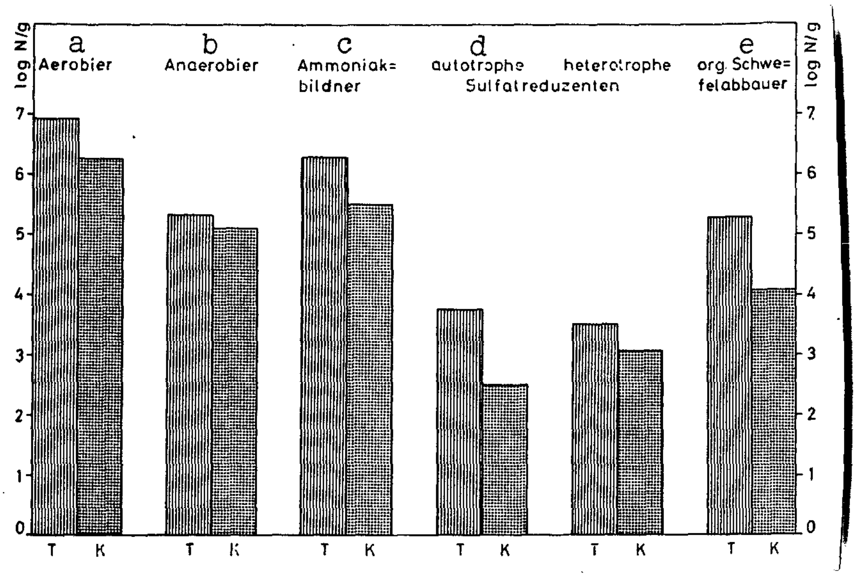

Fig. 4. Comparison of germ counts determined per gram of dry sediment from surface specimens taken at the same point by the diver (T) and with the grab bucket (K). The moist sediment of the top 4 mm was tested.

Key: a. Aerobic organisms
b. Anaerobic organisms
c. Organisms which form ammonia
d. Autotrophic (heterotrophic) organisms which reduce sulfate
e. Organisms which degrade organic sulfur

Location 3 was on a flat sandy surface which contained large numbers of oyster shells. Most of the shells were covered with a sediment of fine sand, however.

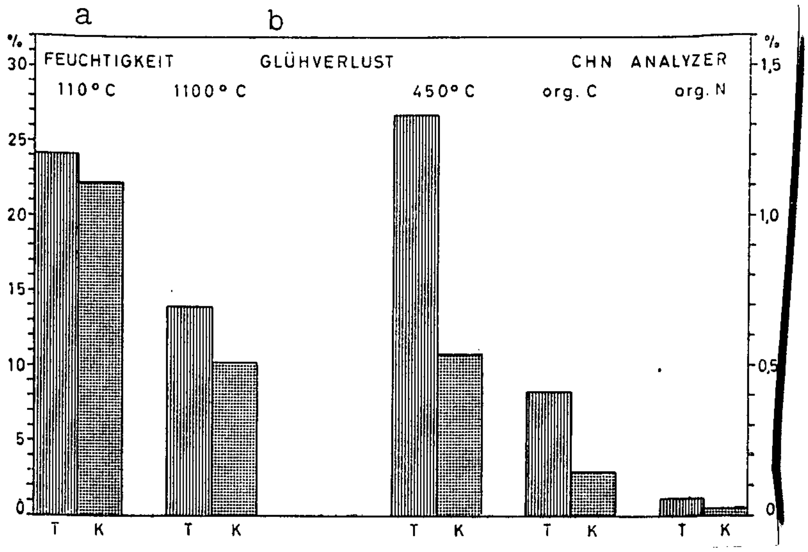

Fig. 5. Comparison of ignition losses and determinations of organic C and organic N (with the CHN analyzer) for specimens taken in parallel by grab bucket (K) and diver (T).

Key: a. Moisture
b. Ignition loss

Location 4 was directly under one leg of the UWL in a recess /463 which the divers normally did not approach.

Location 5 was at the end of the sewage line at a distance of about 100 m from the UWL. The specimens were taken next to the concrete block which held down the end of the sewage line. The sewage was pumped off at irregular intervals. It unfortunately did not prove possible to coordinate pumpoff and sampling in any case, so in the most favorable case, the specimens were taken 3 hours prior to pumpoff and 12 hours after pumpoff. Luckily, a blank value could be taken directly during the laying of the line.

It was found in the course of the project, however, that the germ counts were not significantly altered by the discharging of UWL sewage. However, coli titer was not determined as a sewage indicator.

The most interesting result obtained from this mode of operation was that quite considerable differences in the colonization of relatively similar sediments occur within a very small area (Fig. 6) and that distinct differences occur in the colonization of the uppermost millimeters of sediment when specimens are taken directly at the sediment surface under different tide conditions. Such studies can actually be conducted most easily with the aid of underwater stations, since bottom currents have completely different configurations in areas with large tidal displacements than at the surface and usually can only be determined by direct observation. Theoretically, however, the same result should be achievable with surface /464 divers and a television camera from on board a ship in extremely quiet weather. Particularly in the case of station 2, it was possible to detect a dependence of germ count upon flow during the changing tides (Fig. 6). But the values from station 1 also confirm the fact that the germ counts in sediments are not merely a function of grain-size distribution and organic content, but also of flow conditions.

We have also made an attempt to use several specimens to study the difference in germ count close to the surface for different types of ocean floor coverage. Parallel specimens were taken at locations which had shortly before been covered by a flatfish in order to compare them with specimens taken in the immediate vicinity. The differences were too small, however, to allow precise conclusions to be drawn with the small number of specimens (two paired values). As can be seen from Fig. 5, we also determined microorganisms in the sulfur and nitrogen cycles. The results of these determinations will be discussed within a larger framework, however, along with the results from the utilization of BAH I in the Baltic and further utilization of the UWL, plus a reference series from a ship.

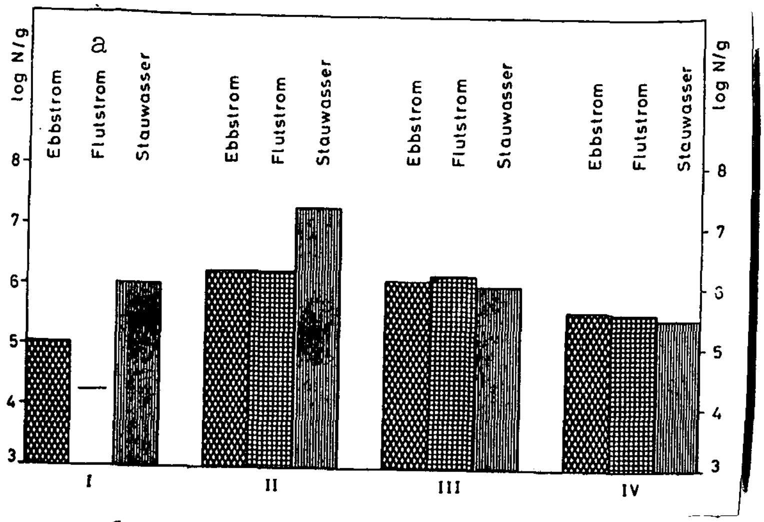

Fig. 6. Comparison of the surface specimens taken at different tide levels at the UWL stations. The germ counts per gram dry material are referred to heterotrophic microorganisms which grow on Zobell's culture medium 2216 E. These microorganisms are capable of mineralizing a large portion of the sedimented organic material.

Key: a. Ebb, flow and slack, respectively

With these unpretentious and relatively modest results from the work of one summer, which are also accompanied by the large number of problems involved in using new instruments and methods for the first time, we have attempted to show how much work is still required from the widest variety of directions in order to arrive at extensive and generally useful data, regardless of the specialized field, in the oceanic milieu.

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